

Appendix H12

Long-term Vegetation Dynamics in Sagebrush Steppe at the INEEL

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Idaho National Engineering and
Environmental Laboratory

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Abstract

Sagebrush (*Artemisia*) steppe is the largest of the semiarid vegetation types in North America, occupying extensive areas of the Columbia and Snake River basins, the northern edge of the Great Basin, and southwestern Wyoming. Nevertheless, sagebrush-dominated communities have been listed among the most endangered North American ecosystems because of losses to agriculture, overgrazing, and invasion by alien annuals. The Idaho National Engineering and Environmental Laboratory (INEEL) occupies some 2,315 km² of sagebrush steppe on the eastern Snake River Plain. Exclusion of domestic livestock from some 990 km² in 1950 and 1957 created the largest of the few protected reserves of this extensive vegetation type.

Permanent vegetation plots were established at the INEEL in 1950 and have been sampled nine times in the intervening years, providing the opportunity to study vegetation dynamics in a large area of natural sagebrush steppe in the absence of grazing by domestic livestock. Here we report patterns of change in cover, density, and distribution of major species and life forms that have occurred over a 45-year period. We analyze data for 47 "core" plots located on central portions of the INEEL in the area closed to livestock grazing and for 32 "peripheral" plots located on the periphery of the INEEL in areas open to livestock grazing. We also assess trends in species richness and relate those trends to total plant cover and variation in cover, and we assess trends in plot similarity through time.

When the first vegetation samples were taken in 1950 and 1957, the area was in the depths of a severe drought; in the 2 decades preceding 1957, annual precipitation exceeded the long-term mean only four times. On the core plots, total cover of shrubs and perennial grasses was only 18% in 1950 and the vegetation was heavily dominated by shrubs, especially *Artemisia tridentata*, which contributed 89% of the shrub cover. Perennial grasses covered only 0.5% of the ground in 1950. In response to increased precipitation, shrub cover increased by from 17% in 1950 to 25% by 1965, and an exponential increase in the abundance of perennial grasses resulted in a 13-fold increase from 0.46% to 6.2% by 1975. Subsequently, shrub cover has fluctuated between 18% and 24% and that of perennial grasses between 1.4% and 4%. The sampling frequency is not adequate to determine how closely variation in cover corresponds to that of precipitation, but correlation analyses indicate that there may be lags of from 3 to 5 years in the response of species

or functional groups to precipitation patterns. Variation in the cover of perennial grasses and that of shrubs was out of phase in the three most recent censuses.

Other than the increase in cover of perennial grasses during the first 25 decades and the general increase in average species richness, we found little evidence of directional changes in plant species composition. The only obvious directional change among the common shrub or perennial grass species was a consistent increase in the cover of *Chrysothamnus viscidiflorus*. There was no evidence of seral replacement among the perennial grasses, nor did members of this functional group tend to respond in concert through time.

The distribution of *Bromus tectorum* at the INEEL expanded rapidly in the decade between 1965 and 1975. This occurred on the core plots in the absence of any major disturbance, demonstrating that *B. tectorum* can invade native vegetation without facilitation by disturbances such as livestock grazing or fire. However, vigorous populations of native species appear to be limiting the abundance of this exotic species, even on most recently burned areas. Although its presence does not appear to be a major threat to the integrity of most INEEL plant communities in the core area at this time, *B. tectorum* has become a dominant on isolated patches and on some areas that have been heavily grazed by sheep in recent years. Further research and monitoring are necessary to better assess its potential for facilitating the conversion of natural shrub steppe at the INEEL to fire-prone annual communities.

Species richness across all plots has not changed appreciably since 1950, but the mean number of species of shrubs, perennial grasses, and perennial forbs recorded per plot has generally increased over the 45-year period. This indicates that populations that were small and isolated in 1950 have increased in size and distribution. The period has also evidenced a substantial increase in heterogeneity in vegetative structure among sample plots. We were unable to find any evidence of common trajectories of vegetation change among plots. Mean percent similarity of the core plots decreased from 72% in 1950 to 40% in 1995. Thus, as the number of species per plot increased, the plots diverged in terms of their species composition and vegetative cover. We believe that these trends are largely the result of 1) recovery of vegetation from drought and grazing as once depleted populations increased in size, 2) an increase in the extent to which fine-scale variation in resource availability influenced the distribution and abundance of species, and 3) the effects of stochastic factors that influenced propagule dispersal and the colonization of safe

sites. The data clearly show that a large-scale perspective is necessary to understand the vegetation dynamics of this shrub steppe.

Vascular plant cover was positively correlated with mean species richness of shrubs, of perennial grasses, and of the two groups combined. The relative change in cover from year to year was negatively correlated with shrub and perennial grass species richness. These patterns are consistent with the hypothesis that higher richness results in more efficient or thorough use of limiting resources. Alternatively, higher richness may reflect higher resource availability and/or increased probability of a species being present that can take advantage of prevailing environmental conditions.

In general, the same kinds of changes have occurred on the core and peripheral plots, indicating that the same mechanisms have been responsible for the roughly parallel changes since 1950. These include a large increase in shrub cover during the first 2 to 3 decades, large increases in the abundance of perennial grasses since 1950, increases in mean richness per plot, and an increase in heterogeneity among plots. The overall structure of the vegetation on the two groups of plots was also quite similar at the latest sampling.

We emphasize that it is not appropriate to construe this in any way as a study of the effects of livestock grazing. The peripheral plots are not a representative sample of the area open to livestock grazing, and data are not available on class of stock, intensity of grazing, or season of use for individual plots over the 45-year period. Furthermore, differences in elevation and in heterogeneity between the core and peripheral plots would confound any such analysis.

Designation of the INEEL as a National Environmental Research Park in 1975 emphasized its importance as a field laboratory for ecological research. The sheer size of the core area makes it unique among protected areas of sagebrush steppe, an area large enough to study landscape-level processes and to accommodate natural population fluctuations and disturbance regimes. The core area should be managed as a natural preserve, insofar as possible. Anthropogenic disturbances should be minimized, exclusion of livestock from the core area should be continued, introduction of non-native species should be minimized, and an aggressive weed control program should be implemented.

Introduction

Large portions of the Columbia and Snake River Plateaus, the northern edge of the Great Basin, and southwestern Wyoming are covered by sagebrush steppes (West 1983a). These communities are characteristically dominated by woody members of the genus *Artemisia* and perennial bunchgrasses. West (1983a) estimated that sagebrush steppes occur on some 4.48×10^5 km², making this the largest "ecosystem type" of the North American cold deserts. Similar sagebrush-dominated communities occupy about 1.8×10^5 km² of the Great Basin and Colorado Plateau where non-halomorphic soils prevail, except that perennial herbaceous species are generally less abundant (West 1983b). It is thought that the relative proportions of grasses and shrubs that existed under pristine conditions in these steppes reflect the degree of aridity of the site, with more xeric conditions favoring dominance by sagebrush and companion shrubs (West 1983a).

The semi-arid, continental climate of the region occupied by the sagebrush steppes is characterized by large diurnal and seasonal temperature fluctuations (West 1983a, Caldwell 1985, Smith et al. 1997). During summer, low humidities and clear skies result in high temperatures and high evaporative demand during the day, while at night rapid radiative cooling produces relatively low temperatures. Winters are cold, with several months having mean temperatures below freezing; however, mountain ranges to the north prevent most polar air masses from reaching the area (West 1983a). Snow cover may persist for periods from weeks to over 2 months. Most precipitation is derived from air masses moving off the Pacific Ocean. West (1983a) reported an average annual precipitation of 246 mm for selected stations. Roughly 60% of the precipitation falls between October and April, much of it as snow; melting snow and spring rains account for most of the annual recharge of soil moisture (Caldwell 1985, Anderson et al. 1987). Summers are very dry, particularly in western portions of the region (West 1983a), and precipitation from summer storms results only in wetting of the top few centimeters of the soil profile (West 1988, Caldwell 1985). Potential evapotranspiration greatly exceeds precipitation, and all of the plant-available soil moisture is used each year (Campbell and Harris 1977, Anderson et al. 1987). The predictability of the annual cycle of moisture availability apparently has selected for similar patterns of water use among the dominant species (Caldwell 1985, Anderson et al. 1987).

Where water for irrigation is available, arable portions of the original sagebrush steppe have largely been converted to agriculture; the remainder is used primarily for livestock grazing. Livestock were introduced to the region in the mid 1800's, and by the end of the century the grazing capacity of most sagebrush-dominated rangelands had been exceeded (West 1983a). Native perennial grasses and many native forbs are highly palatable and nutritious, and moderate to heavy grazing by livestock typically increases dominance by unpalatable shrubs such as sagebrush. Hull (1976) estimated that the loss of native perennial grasses and corresponding increase in shrub cover required only 10 to 15 years of heavy livestock use. Sagebrush steppe rangelands continued to support large numbers of livestock through the first half of this century, and degradation of the plant communities on much of the area was severe (West 1983a). The original grazing capacity of these ranges was estimated as 0.83 animal unit months (AUM) per ha, whereas the capacity in 1970 was estimated to be 0.29 AUM ha⁻¹. Although stocking rates generally have been reduced since the 1930's, most of these rangelands are still used for livestock grazing and many have shown little recovery.

Alien annual species, especially cheatgrass (*Bromus tectorum*), rapidly invaded overgrazed rangelands during the early 1900's (Klemmedson and Smith 1964, Mack 1981). Mack (1981) reported that *B. tectorum* was omnipresent on some 410,000 km² of the Intermountain West, and on many rangelands it was the dominant species. Dense stands of *B. tectorum* and other annuals have greatly increased the fire frequency on sagebrush rangelands (Klemmedson and Smith 1964, Young and Evans 1978, Brown and Minnich 1986, Whisenant 1990, Knick 1999), virtually eliminating perennial shrubs from the communities in some areas. These conversions to an annual system appear to be irreversible (Daubenmire 1970, Young and Evans 1973, Knick 1999), not unlike the annual grasslands of California.

Despite their areal extent, sagebrush-dominated communities are among North America's critically endangered ecosystems as a consequence of losses to agriculture, conversions to exotic annual communities, or degradation due to severe overgrazing (Noss et al. 1995, Christensen et al. 1996). Few relicts of sagebrush steppe that have not been heavily grazed by domestic livestock exist, but those that have been studied provide some indication of the composition and potential productivity of these rangelands (Passey et al. 1982, Kindschy 1994). Such studies may provide a very biased view of presettlement vegetation, however, because the selection of sites is based largely on the investigator's perceptions of pristine. Few data are available that provide

insight into the spatial heterogeneity or variation in composition that might have existed in presettlement times. West (1983a) noted that sagebrush may contribute up to 70% of the plant biomass on sites that have not been grazed. Some ungrazed kipukas in southeastern Idaho have nearly pure stands of sagebrush, while others support communities that are dominated by perennial bunchgrasses and have abundant forbs (JEA, personal observation). The studies of Passey et al. (1982) show that annual productivity varies strongly with climatic conditions, including conditions of the preceding year or two. Passey and Hugie (1963) reported a three-fold year-to-year variation in peak biomass. Variations of even higher magnitude have been reported in communities dominated by *B. tectorum* (Klemmedson and Smith 1964) and stands of the introduced crested wheatgrasses (*Agropyron cristatum* and *A. desertorum*) (Sneva 1973, Sharp et al. 1992) in the sagebrush steppe region. Above-ground productivity of a stand of *A. cristatum* and *A. desertorum* in southern Idaho varied from 150 to 1200 kg/ha over a 35-year period; 72% of the variability was accounted for by variation in May-June precipitation (Sharp et al. 1992). Aside from these studies, we know little of the magnitude or mechanisms of long-term variations in productivity or species composition in the absence of livestock grazing.

In 1950 and 1957, 2315 km² of sagebrush steppe on the upper Snake River Plain were purchased or withdrawn from the public domain to form what is now designated as the Idaho National Engineering and Environmental Laboratory (INEEL; Fig. 1). About 43% of the area has been closed to grazing by domestic stock since at least 1957. Most of that area was closed to grazing in 1950, and grazing likely was restricted on much of it while it was used as a Naval gunnery range during World War II. The absence of anthropogenic disturbances over most of the area, coupled with data from permanent vegetation plots, provides a unique opportunity to study vegetation dynamics in a large area of natural sagebrush steppe.

Here we present analyses of data collected between 1950 and 1995 from permanent vegetation plots. The objectives of this study were to:

1. Describe patterns of change in cover, density, and distribution of major species and life forms that have occurred over the 45-year period
2. Determine the relative contributions of shrubs, perennial grasses, perennial forbs, and annuals to total vascular plant cover after 45 years without livestock grazing.

3. Examine the magnitude of fluctuations in species abundance that might be expected in a sagebrush steppe in the absence of major anthropogenic or natural disturbances.
4. Determine whether changes in the abundance of major species or life forms are related to precipitation patterns.
5. Assess trends in species richness and determine whether total plant cover or variation in cover through time is related to species richness.
6. Determine whether there is a relationship between total shrub cover and total grass cover.
7. Assess changes in plot similarity through time.
8. Compare trends for the area that has been closed to livestock grazing to those in the area open to livestock.

Study Area

The INEEL lies at an average elevation of about 1500 m on the western edge of the upper Snake River Plain in southeastern Idaho, USA (43° N, 112° W) (Fig. 1). The area lies in the rain shadow of the numerous mountain ranges of central Idaho. Average annual precipitation is 220 mm. Precipitation tends to be uniformly distributed throughout the year except for a strong peak early in the growing season (Fig. 2). On average, 37% of the annual precipitation falls during April, May, and June; May and June are the wettest months (Fig. 2). The frost-free period averages about 90 days but has ranged from 68 - 123 days over 45 years of record.

The Snake River Plain was formed by the eruption and emplacement of great masses of volcanic rock (Nace et al. 1972). Surface features at INEEL that reflect a long history of volcanic activity include three prominent buttes and some 22 well defined cones, craters, and vents (Nace et al. 1972). Most of the area occupied by the INEEL is a relatively flat plain, but the terrain is frequently broken and undulating because of underlying basalt flows. Lava outcrops are common. Weathering and erosion have had little impact on the original morphology of the emplaced lava (Nace et al. 1972); thus most INEEL soils are of aeolian origin derived from older silicic volcanics and Paleozoic rocks from the surrounding mountains (McBride et al. 1978). Accumulations of sand on lee sides of outcrops, in depressions, and on dunes result in abrupt gradients in soil texture that may influence plant species composition over relatively short

distances (Shumar and Anderson 1986). INEEL soils are primarily orthidic Aridisols, with Calciorthids being the most common great group. Entisols, namely Torriorthents and Torrifluvents, and Mollisols, including Calcixerolls, are also common.

Vegetation at the INEEL typically is characterized by an overstory of big sagebrush (*Artemisia tridentata*), two subspecies, *A. t. wyomingensis* and *A. t. tridentata*, are common (Shumar and Anderson 1986). Other common shrubs include *Chrysothamnus viscidiflorus*, *Leptodactylon pungens*, *Gutierrezia sarothrae*, and *Grayia spinosa*. Perennial grasses, including *Pseudoroegneria spicata*, *Elymus lanceolatus*, *Elymus elymoides*, *Oryzopsis hymenoides*, and *Stipa comata*, are typically the most abundant herbaceous perennials, but the area also supports a diversity of forbs (Table 1). Anderson et al. (1996) provided a general description of the vegetation and a complete flora.

Use of the area occupied by the INEEL prior to 1950 is not well documented. Much of the upper Snake River Plain has been grazed by livestock since the late 1800's (Harniss 1968). The area was crossed by a trail used for moving cattle to eastern markets during the late 1870's, and it was used extensively for spring and fall sheep grazing. Harniss and West (1973a) concluded that the area was severely overgrazed prior to 1950. The low cover of perennial grasses in 1950 supports that conclusion (Anderson and Holte 1981), but, as shown below, prolonged drought during the 1930's and 40's may have exacerbated grazing impacts.

Although domestic livestock have been excluded from a portion of the area since 1950, native herbivores are common and sometimes very abundant. The area provides winter range for large numbers of pronghorn (*Antilocapra americana*), some pronghorn and a few mule deer (*Odocoileus hemionus*) are yearlong residents. Elk (*Cervus elaphus*) colonized the INEEL during the mid 1980's (Moritz 1988), and two herds of about 80 animals each were present by 1989 (Strohmeyer 1992). Since then, numbers have varied in annual censuses from 53 in summer to over 350 in winter (R. Warren, unpublished data). Populations of black-tailed jackrabbits (*Lepus californicus*) are cyclic, reaching high densities at approximately 10-year intervals (Anderson and Shumar 1986). The most recent noteworthy peak in the jackrabbit population occurred in 1981 when densities reached approximately 2 jackrabbits/ha. Except for a minor increase in the early 1990's (Porth 1995), jackrabbit populations have been very low since 1983 (J. Anderson and R. Warren, unpublished data). Scattered populations of cottontail rabbits (*Sylvilagus nuttallii*) and

pygmy rabbits (*Sylvilagus idahoensis*) also exist (Wilde 1978), and small mammals can be locally abundant (Groves and Keller 1983).

Methods

Precipitation Data and Estimates. Precipitation data from the station at the INEEL Central Facilities Area are available from 1950 to present. To estimate INEEL precipitation prior to 1950, data from 1950 through 1990 from three surrounding locations, Arco, Blackfoot, and Idaho Falls, were used as independent variables in a stepwise multiple regression with actual INEEL precipitation as a dependent variable. The independent variables that explained the greatest amount of variance in the actual INEEL precipitation were used to estimate precipitation from 1905 to 1949. This process was done separately for total annual (September through August) and for growing season (April through July) precipitation. Data from Arco and Blackfoot together explained the greatest amount of variance in INEEL precipitation. For years in which data from one or both of these sites were missing, data from the available sites were used to estimate INEEL precipitation. Average annual and growing season precipitation were calculated using estimated and actual INEEL data from 1905 through 1986. Five-year sliding averages were calculated by averaging precipitation in the current year with that in the 4 preceding years.

Permanent Vegetation Plots. Vegetation studies were initiated at the INEEL in 1950 with the establishment of 94 permanent sample plots along two perpendicular lines (Fig. 1). Most of these were at 1.6-km intervals, but intervals were shorter near the buttes on the southern and eastern sides of the INEEL. Two plots were destroyed prior to 1957. The remaining 92 plots were sampled in 1950, 1957, 1965, 1975, 1985, and 1995. A subset of 35 or 36 plots, corresponding to those analyzed by Anderson and Holte (1981) and Anderson (1986), was sampled in 1978, 1983, and 1990. Other analyses of data from these plots include Harmiss (1968) and Harmiss and West (1973a,b).

Forty-three plots are within the area that is closed to livestock grazing (Fig. 1). We included four additional plots as "closed" because they have been inaccessible to livestock since the INEEL was established (see Appendix). This closed area comprises the central portions of the INEEL, which lie at the lowest elevations. The absence of *Pseudoroegneria spicata* over most of this area indicates that it is generally more arid than the periphery. Anderson and Holte (1981) subjectively chose 36 of these plots thought to be representative of reasonably homogeneous sites

and vegetation for analyses of long-term trends. For the current study, we performed numerous cluster analyses and ordinations of the data from all 47 plots within the closed area and all years. These analyses failed to confirm the 36-plot selection or to identify a consistent homogenous subset of plots (results not shown). Therefore, we used data from all 47 plots for the current analyses whenever possible. We refer to these as the **core** plots. For some analyses, we used data from the 35 core plots that were sampled in every census year.

The remaining plots, which we refer to as **peripheral**, are at more diverse elevations and therefore sample much more heterogeneous vegetation. Many of these plots lie at higher elevations than the core plots; the presence of *Pseudoroegneria spicata* and *Artemisia tripartita* indicates that they lie in areas receiving higher precipitation. Other peripheral plots on the northeast end of the longer transect (Fig. 1) are at lower elevations and support salt-desert vegetation. Although these plots all lie within the area that is open to livestock grazing, they cannot be considered a representative sample of that area, for they sample along only four short transects within that large area (Fig. 1). Furthermore, they are heterogeneous with respect to type of livestock and season of use. Plots on the north and east sides of the INEEL typically are grazed by sheep in the spring and/or fall and winter. Plots on the south and west sides usually have been grazed by cattle during spring and summer, but recently the west side has been grazed by sheep early in the season. There are no records of intensity of use for individual plots, but it seems safe to assume that proximity to water and/or roads would have resulted in very different levels of use from plot to plot and from year to year. While sampling over the past 2 decades, we have seen evidence of livestock use on some plots in some years, while there are others where we have never seen evidence of livestock. For the analyses included herein, we included data from all of the plots within the area open to livestock grazing with the exception of seven plots on steep portions of Big Southern Butte, one steep plot on East Butte, and two plots in areas that were plowed and seeded to *Agropyron desertorum*. This left a sample of 32 peripheral plots. We emphasize that because of the differences in environment and in heterogeneity between the core and peripheral plots, and because of the other confounding factors mentioned, it is not possible to draw inferences or conclusions regarding the effects of grazing since 1950. Although we compare the trends on the core and peripheral plots, this effort must not be construed as a grazed vs. ungrazed area study.

For some analyses concerning relationships between species richness and cover or change in cover, we combined data from the core and peripheral plots. Here, we were looking for landscape scale patterns, and, because vegetation trends were similar on the core and peripheral plots, we saw no reason to not include peripheral plots to make the sample as large as possible.

Vegetation Sampling. Cover, density, and frequency were assessed during June, July, and August, according to the original sampling design (see Anderson et al. 1978 for details). Two parallel 15 24-m transect lines were established in 1950 at each plot (Fig. 1). Crown cover of shrubs and basal cover of perennial grasses were measured by line interception (Canfield 1941) along the two transect lines (in the original sampling design, cover estimates were limited to shrubs and perennial grasses). Ten density quadrats (each 0.3 x 1 m) were located at 1.52-m intervals along each transect line. Density of all perennial species was recorded for each of the 20 quadrats, annuals were inventoried in a 0.1 x 0.1-m subsection of each quadrat.

Because the original sampling design did not estimate abundance for all growth forms on a common scale, we estimated cover in 1985 and 1995 by point interception (Floyd and Anderson 1982). A 0.5- x 1-m point sighting frame, with 36 points at 0.1-m intervals, was centered at 1-m intervals over a taut tape. The plant species or other entity (e.g. bare ground) under each point was recorded to estimate canopy cover of shrubs and forbs and basal cover of graminoids. Fifteen frames were examined on each of the original transect lines; 20 additional frames were examined on a third line 20 m in length, providing a total sample of 50 frames per plot. The 20-m line was parallel to the original transects, 4.57 m from the line farthest from the plot identification stake. We used these data to estimate the relative contributions of shrubs, perennial grasses, perennial forbs, and annuals to vegetal cover. We compare vegetative structure of the core plots using data for 1985 and 1995, and we compare structure of core with peripheral plots using 1995 data.

Data Analyses. Because of discrepancies in the identification of grass species formerly classified in the genus *Agropyron* and in the genus *Poa* by different investigators over the 45-year period, the species in each of these groups were pooled for the current analyses. For convenience, we refer to the first group as the "agropyrons," included are *Pseudoroegneria spicata*, *Elymus lanceolatus*, and *Pascopyrum smithii*. Of these species, *Elymus lanceolatus* is by far the most abundant and widespread on the core plots.

For analyses of density data from 1950 and 1957, the sample size was less than 47 because the original data sheets are missing. We have no density data for plot 82 in 1950 and for plots 86 and plot 88 through 93 for 1957. Thus, the sample size for density analyses was 46 for 1950 and 40 for 1957.

We tested for relationships between cover and precipitation using both annual (September through August) and growing season (April through July) precipitation. For each of the more abundant species or species groups, cover was correlated with precipitation in the census year, with precipitation in each of the 5 years preceding the census year, and with precipitation of the census year averaged with 1 to 4 preceding years. Sample size for these analyses was nine, with each point representing average cover on the 47 core plots and precipitation for a single year or average. The resulting relationships were compared to see which value for precipitation was the best predictor of average cover.

We addressed relationships between cover and species richness in two ways, and separately for shrubs and for perennial grasses. First, for each sample year we correlated total cover of shrubs or perennial grasses with species richness of the same group on individual plots. Sample sizes for these analyses ranged from 34 to 79 plots, depending on the number of plots that were sampled in a given year. Second, we correlated average cover of shrubs and of perennial grasses over the 9 census years with average species richness of each group over the same 9 years. For this analysis we used the subset of 35 plots that was sampled in each of 9 sample years.

We also asked whether variation in cover of shrubs or perennial grasses was correlated with species richness of those groups. This question was addressed in two ways. First, we calculated change in cover by taking the absolute value of the change in cover of all shrubs, or all perennial grasses, between each adjacent pair of censuses and averaging those 8 values for each plot. We then correlated average change in cover with average species richness for the 9 census dates. We performed this analysis for the subset of 35 plots that were sampled at every census, and also for a subset of the 79 plots that were sampled in 1950, 1957, 1965, 1975, 1985, and 1995. Second, we calculated standard deviation and coefficient of variation of cover separately for shrubs and for perennial grasses and correlated those values with average species richness for the same 9 sample years. This analysis was performed for the subset of 35 plots that were sampled at every census. In addition to these analyses of relationships between species richness and cover or

change in cover, which were done separately for shrubs and for perennial grasses, we performed similar analyses for combined cover and species richness of shrubs and perennial grasses.

To assess changes in similarity among plots through time we calculated percent similarity (PS = sum of minimum proportional abundance of each species) of plots that were sampled in each census year. PS was calculated for each pair of plots and the average of all pairwise indices was calculated for each year. These annual averages were then plotted against time.

Results

Long-term trends in precipitation. In 1950 when the first vegetation samples were taken at the INEEL, the area was in the depths of an intense drought; in the 2 decades preceding the 1957 census, annual precipitation exceeded the long-term mean only four times (Fig. 3). Five-year sliding averages show a generally decreasing trend in total annual as well as growing season precipitation from the early 1900's through the mid 1950's, and they clearly indicate the duration and severity of the drought in the 1930's, 1940's, and early 1950's (Fig. 3). After 1955, precipitation increased markedly, and the sliding averages generally were above the long-term averages from the late 1950's through the mid 1970's. Drought in the late 1970's was followed by above average precipitation in the early 1980's. Drought prevailed again in the late 1980's and early 1990's, but 1993 and 1995 were exceptionally wet years (June of 1995 was the wettest month of record at the Central Facilities Station). The five-year sliding average of annual (September 1 - August 31) precipitation is plotted for reference on some figures that follow.

Vegetal Composition of Core and Peripheral Plots. Table 1 summarizes cover data collected in 1985 and 1995 by point interception. Despite relatively high precipitation in the early 1980's, total vascular plant cover was much higher in 1995 than in 1985 on the core plots (24% in 1985 vs. 38% in 1995). Although absolute shrub cover differed little between the 2 years, shrubs contributed 74% of the total cover in 1985 but only 50% in 1995. Graminoid cover more than doubled in the decade and relative cover of graminoids increased from 10 to 15%. Absolute cover of perennial forbs was also more than two-fold higher in 1995 than in 1985, and their relative cover increased from 5.2 to 7.7%. The largest difference in absolute cover between the 2 sample years was that of annuals and biennials, which was over four times higher in 1995; relative cover of this group increased from 10 to 25%. Cover of introduced annuals and biennials was 13 times higher in 1995 than in 1985.

In 1995, total vascular plant cover was nearly identical on the core and peripheral plots (Table 1). The contributions of shrubs and perennial grasses to total cover were also quite similar on the core and peripheral plots (Table 1). Fourteen species of shrubs were recorded in the point frame data on the peripheral plots, compared with 11 on the core plots. Four species of *Artemisia* occurred on the peripheral plots, while only *Artemisia tridentata* was recorded on the core plots, reflecting the much greater habitat diversity on the peripheral plots.

Perennial forbs contributed 10.3% of the vascular plant cover on the peripheral plots in 1995 (Table 1), compared to 7.7% on the core plots. However, the largest difference between the two sets of plots was in cover of annuals and biennials. In 1995, this group contributed 25% of the vascular plant cover on the core plots, but only 13% on the peripheral plots. The cover of native and introduced annuals and biennials on the core plots was essentially equal in 1995, whereas on the peripheral plots native annuals and biennials produced twice the cover of introduced ones (Table 1). On both core and peripheral plots, there were more native annual and biennial species than introduced ones. Twenty-seven native species of annuals and biennials were recorded on the core plots in 1995, compared with nine introduced species. On the peripheral plots, there were 22 native and 10 introduced species.

Bromus tectorum was present on nine of 27 peripheral plots at the first census in 1950 and was recorded on nearly half of the peripheral plots in 1995 (Table 2). *B. tectorum* was not recorded on any core plot prior to 1975, but was recorded on more than 50% of the core plots sampled in 1990 and 1995. As the most abundant annual on the core plots in 1995, *B. tectorum* accounted for 6.6% of vascular plant cover (Table 1). Since 1985, the range of *B. tectorum* densities on the core and peripheral plots has been similar, much higher densities were recorded on some peripheral plots prior to 1985 (Table 2).

Long-term trends in plant cover. Shrubs have dominated cover on the core and peripheral plots in all sample years (Fig. 4). On the core plots, shrub cover ranged from 17% in 1950 and 1957 to a high of 25% in 1975. A similar trend occurred on the peripheral plots (Fig. 4). In both cases, the dominant shrub was *Artemisia tridentata*, which contributed 84% of the shrub cover on the core plots in 1950. *A. tridentata* contributed much less to total cover on the peripheral plots (Fig. 4) where there is a larger diversity of shrubs across the sample plots (Table 1). The decrease in shrub cover after 1975 (Figs. 4, 5) was due to widespread die-off of *A. tridentata*.